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Research report

Individual variation in the propensity to attribute incentive salience to a food cue: Influence of sex

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HIGHLIGHTS

- Two different outbred strains: Sprague-Dawley and Heterogeneous Stock.
- Motivational value of the cue was assessed by two measures.
- Female SD rats acquired PCA behavior slightly faster than males, but not in HS rats.
- No sex difference or any impact of estrous cycle in asymptotic PCA behavior.
- Females had more active/inactive responses in the conditioned reinforcement test.

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ABSTRACT

There is considerable individual variation in the propensity of animals to attribute incentive salience to discrete reward cues, but to date most of this research has been conducted in male rats. The purpose of this study was to determine whether sex influences the propensity to attribute incentive salience to a food cue, using rats from two different outbred strains (Sprague-Dawley [SD] and Heterogeneous Stock [HS]). The motivational value of a food cue was assessed in two ways: (i) by the ability of the cue to elicit approach toward it and (ii) by its ability to act as a conditioned reinforcer. We found that female SD rats acquired Pavlovian conditioned approach behavior slightly faster than males, but no sex difference was detected in HS rats, and neither strain showed a sex difference in asymptotic performance of approach behavior. Moreover, female approach behavior did not differ across estrous cycle. Compared to males, females made more active responses during the test for conditioned reinforcement, although they made more inactive responses as well. We conclude that although there are small sex differences in performance on these tasks, these are probably not due to a notable sex difference in the propensity to attribute incentive salience to a food cue.

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1. Introduction

Natural rewards (e.g., food and water) are powerful objects of desire, presumably because they are necessary for survival. However, much behavior directed toward obtaining them is not controlled so much by the reward itself, but by previously neutral stimuli (conditioned stimuli, CSs) that have been associated with them—i.e., sights, sounds and places that predict the availability and location of rewards. That is, if CSs are attributed with incentive salience they acquire the ability to act as incentive stimuli, and as such, attract animals toward them, often bringing them into close proximity with the reward itself [1–3]. In addition, incentive stimuli can arouse complex emotional and motivational states that serve to instigate motivation for them, and their associated reward, again facilitating the probability a reward will be sought and procured [4–7].

Animals vary in their propensity to attribute Pavlovian conditioned motivational properties ('incentive salience') to discrete reward cues. It has been reported, using a so-called 'autoshaping' procedure, that a cue (lever) associated with a food reward becomes

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attractive – eliciting approach toward it – only in some animals (sign-trackers, STs) [8–15]. Upon presentation of a lever-CS other animals go to the location of impending reward delivery (these animals are called goal-trackers, GTs) [10]. Thus, the lever-CS acquires one property of an incentive stimulus, attractiveness, to a greater extent in STs than GTs, and this predicts whether a food cue acquires other properties of an incentive stimulus [16–18]. For example, discrete reward cues arouse greater conditioned motivation, and act as a more effective conditioned reinforcer, in STs than GTs [19–21]. It has been suggested, therefore, that although a discrete food cue acts as an effective CS in both STs and GTs (i.e., it attains predictive value for both), it is attributed with greater incentive salience in STs. Interestingly, the propensity to approach a food cue also predicts the extent to which discrete drug cues acquire incentive motivational properties [13,20,22].

Previous studies on individual variation in the propensity to attribute incentive salience to reward cues have been conducted using male animals (mostly rats). There is, however, a great deal of clinical and preclinical research indicating that females are more responsive to both nondrug [23,24] and drug rewards than are males [25–33], and that this increased responsive may be due to circulating sex hormones [34]. Drug self-administration studies have shown that females respond more than males through extinction and reinstatement procedures [35]. With regards to nondrug reward, [23] demonstrated that female rats more readily acquired a goal-tracking response to a tone-CS, and were initially more resistant to extinction, compared to males. These studies suggest, therefore, that female rats may be more prone to attribute incentive salience to a reward cue than males. To further explore this hypothesis we quantified the extent to which a discrete food cue (lever-CS) acquired two properties of an incentive stimulus: (i) the ability to attract and (ii) the ability to act as a conditioned reinforcer, in male and female rats of two different outbred rat strains, Sprague-Dawley (SD) rats and heterogenous stock (HS) rats.

2. Methods

2.1. Animals

Five-week old male (105–125 grams upon arrival) and female (90–110 grams upon arrival) SD rats were obtained from Harlan Laboratories (Indianapolis, IN, USA). These rats were acquired as litters, totaling 9 litters of male and female siblings ($n = 5$–6 each sex per litter, total $n = 48$/sex). Male (5–7 weeks old, 98–186 grams, $n = 24$) and female (5–7 weeks old, 86–143 grams, $n = 25$) HS rats from 11 different litters were acquired from the Medical College of Wisconsin. The National Institutes of Health (NIH)-derived HS rat colony at the Medical College of Wisconsin is comprised of outbred animals derived from a set of eight genetically and phenotypically diverse inbred founder strains: ACI/N, BN/N, BUF/N, F344/N, M520/N, MR/N, WKY/N, WN/N. These founder strains were selected because they represented a relative broad spectrum of laboratory rats' genomic differences and at least some were of independent origin [36,37]. The HS rat colony has been maintained using a relatively large number of breeders (46 breeder pairs) and uses a circular breeding scheme in an effort to decrease inbreeding [37] which may, in part, explain their increased phenotypic variation.

Upon arrival, all rats were housed in same-sex pairs in Plexiglas cages and kept on a 12-h light/12-h dark cycle (lights on at 0800 h) with regulated temperature and humidity. Food and water were available ad libitum. The day prior to the first Pavlovian training session, SD males and females were 275–325 g and 135–165 g, and HS males and females were 210–310 g and 135–200 g, respectively. These weights correspond to roughly the same age in males and females. In order to determine stage of estrous cycling in a subset of SD females, (unstained) vaginal epithelial cells were examined daily via light microscope for at least 10 consecutive days beginning 2 days prior to onset of behavioral testing [38]. Males were handled daily during this time. All procedures were approved by the University of Michigan Committee on the Use and Care of Animals.

2.2. Pavlovian conditioned approach

2.2.1. Conditioning chambers

Med Associates test chambers (20.5 cm × 24.1 cm floor area, 29.2 cm high; Med Associates, St. Albans, VT) were used for Pavlovian training. Each chamber was equipped with a food receptacle located in the center of the 20.5 cm wall, 2.5 cm above the floor. A catch tray filled with corn-cob bedding was located underneath the floor, which was constructed from stainless steel rods. An illuminated retractable lever (Med Associates) was located approximately 2.5 cm to the left or right of the food receptacle, 6 cm above the floor. The side of the lever with respect to the food receptacle was counter-balanced across boxes to eliminate any side bias. A red house light was located on the wall opposite the food receptacle and remained on for the duration of training sessions. A white LED was flush-mounted on the inside of the lever and was used to illuminate the slot through which the lever protruded. The lever required a 10 g force to deflect, such that most contacts with the lever were recorded as a 'lever press'. The pellet dispenser (Med Associates) delivered 1–45 mg banana-flavored food pellet (Bio-Serv®, no. F0059, Frenchtown, NJ) into the food receptacle at a time. Head entry into the food receptacle was recorded each time a rat broke the infrared photobeam located inside the receptacle (approximately 1.5 cm above the base of the food cup). Each conditioning chamber was located in a sound-attenuating enclosure and background noise was supplied by a ventilating fan to mask outside noise.

2.2.2. Pavlovian conditioning procedures

Rats were acclimated to the colony room for several weeks and handling occurred on a regular basis before training procedures commenced. All training sessions were conducted during the 12-h lights on period. Prior to the start of training ~20 banana-flavored food pellets were placed into the rats' home cages to familiarize the animals with this food. For pre-training rats were placed into the test chamber and red light remained on yet the lever remained retracted. Twenty-five food pellets were delivered on a variable interval (30 s) schedule in order to determine whether rats were reliably retrieving the pellets from the receptacle. By the end of the pre-training session, all rats consumed all of the food pellets. Pavlovian training began the following day using a procedure similar to that described previously [39]. During a Pavlovian training session, each individual trial consisted of the insertion of the illuminated lever (CS) into the chamber for 8 s, and immediately following the retraction of the lever the pellet dispenser was activated causing the delivery of a single food pellet (unconditioned stimulus, US) into the food receptacle. The intertrial interval (ITI) started immediately following the retraction of the lever. The CS was presented on a random interval 90 s schedule (i.e., one presentation of the CS occurred on average every 90 s, but the actual time between CS presentations varied randomly between 30 and 150 s). Each Pavlovian training session consisted of 25 trials, resulting in a 35–40 min session, and training was conducted over 8 consecutive days. We recorded the following events for each trial: (i) number of lever deflections, (ii) latency to first lever deflection, (iii) number of head entries into the food receptacle (referred to as magazine entries) during presentation of the CS, (iv) latency to the first receptacle entry following

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